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# Principles and Problems of Ecology

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# PRINCIPLES AND PROBLEMS OF ECOLOGY AS ILLUSTRATED BY ANIMALS

By VICTOR E. SHELFORD

(*With Six Figures in the Text*)

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## I. Introduction

During the past twenty years plant ecology has made great progress. Nearly all the organization of that science as well as the accumulation of most of its present body of facts has been accomplished during that period. The development of modern animal ecology has been much slower. This is probably due in part to the greater difficulty in obtaining a proper view-point at the beginning and in securing enough data to make the first principles evident.

The present paper is intended to present some of the simpler principles from the view-point of the writer. It is not an attempt to treat the subject

exhaustively. Only illustrative data touching on important lines of ecological work are presented. On the animal side the relations of ecology to structure, to genetics, and to evolution are far from clear, and any discussion of these subjects in this connection would involve futile speculation.

Ecology (**3**) is that branch of general physiology which deals with the organism as a whole, with its general life processes as distinguished from the more special physiology of organs. With these limitations upon the term physiology, what may be termed physiological life histories covers much of the field. Under this head fall matters of rate of metabolism, functional and activity rhythms, latency of eggs, time and condition of reproduction, necessary conditions of existence, quantity of life, and especially behaviour in relation to the conditions of existence. The behaviour reactions of an animal maintain it in its usual environment; reactions are often dependent upon rate of metabolism and other physiological states which may be modified by external conditions. Behaviour reactions so far as they occur and can be determined throughout the life cycle are a good index of a physiological life history.

If we knew the *physiological life histories* of a majority of animals, most other ecological problems would be easy of solution. The chief difficulty in ecological work is our lack of knowledge of physiological life histories. With elaborate facilities these may be worked out in a laboratory. Ecology, however, considers physiological life histories primarily in nature, and for this reason the central problem of ecology is the *mores*[1] problem.

Ecology is divisible into individual ecology or the ecology of individuals or particular species (autecology of Schröter), and when several species belonging to one genus are treated it is sometimes termed aggregate ecology (Adams). Thus individual ecology and aggregate ecology stand in contrast to the ecology of communities (synecology of Schröter).

## II. Characteristic Data in Individual and Aggregate Ecology

In individual ecology we are concerned with physiological life histories. Life histories are, or at least have been, worked out one by one, and thus individual ecology is far older than the ecology of communities. Often only

[1] *Mores* (Lat., sing. *mos*), "behaviour," "habits," "customs"; admissible here because behaviour is a good index of physiological conditions and constitutes the dominant phenomenon of a physiological life history and of community relations. We have used this term just as "form" and "forms" are used in biology, in one sense to apply to the general ecological attributes of motile organisms, in another sense to animals or groups of animals possessing particular ecological attributes. When applied in this latter sense to single animals or a single group of animals, the plural is used in a singular construction. This seems preferable to using the singular form *mos* which has a different meaning and introduces a second word. The organism is viewed as a complex of activities and processes and *mores* is therefore a plural conception.

certain aspects of a physiological life history have been emphasized by an author and serve to illustrate such topics as dormancy, behaviour characters under different conditions, etc.

1. **Differences in ecological characters of individuals of the same animal species, living under different conditions.** The responses of sessile plants to different conditions are usually responses made evident in form and structure. Comparing the air and water leaves of certain amphibious plants we note that the former are entire and the latter divided. The difference in ecological character of individuals of an animal species living in ponds and in intermittent brooks has been studied in the case of a small flat crustacean (Isopoda) called a water sow-bug (*Asellus communis*) by Allee (**6**). The species occurs throughout the eastern half of the United States. Near Chicago the animals are found throughout the year in vegetation-choked ponds and in small streams which sometimes dry in summer excepting for pools. In ponds they are usually near the margins in spring and in deeper water later in the season, where they remain on the bottom during strong light and near the surface during dim light. If the pond dries they burrow into the mud and may thus withstand a drought of several months. In streams they are most often found among bunches of dead leaves and when the current is flowing, especially in protected situations.

Allee studied the reactions of the pond animals and of the stream animals to water current (rheotaxis) in a straight current apparatus (Fig. 1) and in

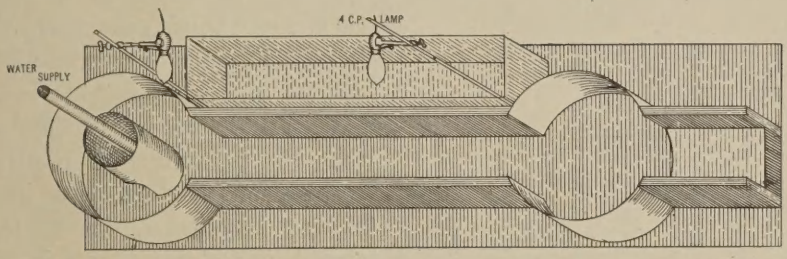


FIG. 1. Allee's straight current apparatus with symmetrical lights and control box. The animals were confined in the central portion of the former by screens.

a circular current produced with the hand in a tin pan. He produced this circular current with much skill and precision and was thus able to study reactions of animals immediately after taking them from the stream or pond. He found that the stream specimens were much more efficient and oriented with heads up stream much oftener than the pond specimens. This difference is shown for the season in Fig. 2 where the percentage of positive orientations is shown by the curves. The marked fall is for the breeding season.

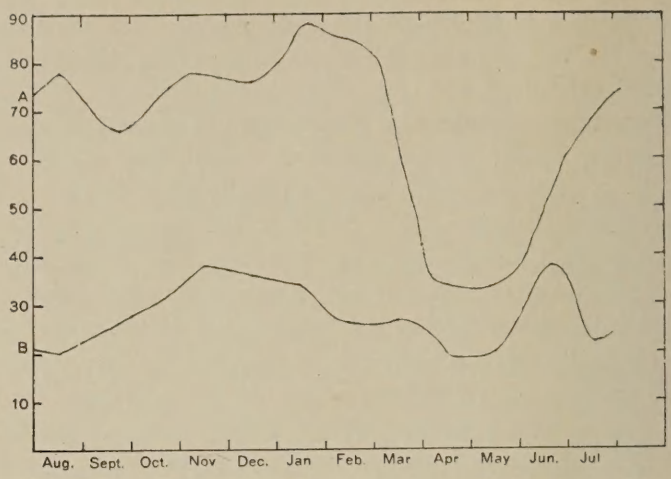


FIG. 2. Showing the rheotactic response of stream isopods (*A*) and pond isopods (*B*) throughout an annual cycle. Vertical distance represents percentage of positive orientations. Note that the two curves are nowhere coincident and that there is a distinct drop during the breeding season in both. (After Allee.)

Allee then undertook to determine the cause of the difference. He first noted that the oxygen content is much greater and the carbon dioxide content much less in the stream than in the ponds. He reared stream isopods in much oxygen and in little oxygen and pond isopods in much oxygen and little oxygen and found that the percentage of positive responses of pond isopods in high oxygen became similar to that of stream isopods as shown in Fig. 3. Also stream isopods in low oxygen became like the pond isopods in low oxygen. The reaction can be reversed even in adults, but the difference is less permanent.

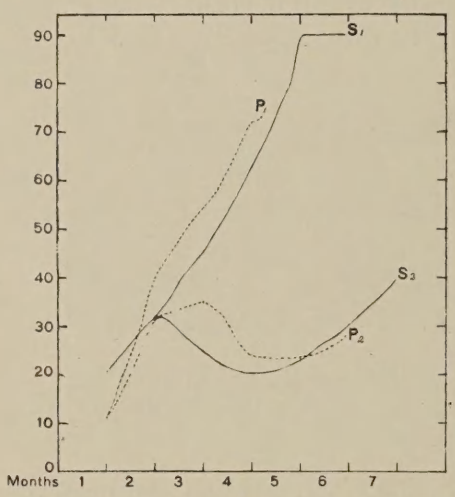


FIG. 3. Showing the modification and reversal of the rheotactic response in isopods during development, by different concentrations of oxygen. $S_1$, stream isopods in high oxygen, $S_2$ in low oxygen; $P_1$, pond isopods in high oxygen, $P_2$ in low oxygen. Note the almost complete reversal. (After Allee.)

He further produced the high oxygen results with agents known to stimulate metabolism and reversed results with agents known to depress metabolism. He found also that pond and stream isopods did not differ in taxonomic characters but differed

in behaviour, size, and vigour. The stream individuals are more vigorous. The difference is not one of inheritance and does not involve the usual taxonomical characters. Hence the different groups cannot be called species or races but are physiological or behaviour groups which we have termed *mores*.

2. **A characteristic physiological life history.** To illustrate physiological life histories we can give a general account of a species of tiger beetle (Cicindelidae). The tiger beetles are brilliantly coloured swift flying insects which live chiefly in open bare ground. *Cicindela hirticollis* will serve to illustrate in the case of land invertebrates. It lives along the beach of lake Michigan on moist clean sand. The adults are much influenced by weather and are active only on warm sunny days. They make burrows in the sand for the night and cloudy, cold or rainy days. Eggs are laid in late June and in July and in low moist places on the beach just beyond the reach of the usual waves. They are deposited in small vertical burrows made by the ovipositor. The female selects the position of a hole or given set of holes after trying the soil and rejecting such places (holes are left incomplete and without eggs) as do not give the proper stimulus (**33**).

To test the soil factors governing egg-laying, animals were placed in cages containing four kinds of soil (**34**). We note from Table I that even under

TABLE I

*Showing egg-laying of* Cicindela *in a cage containing four kinds of soil*

| | | Sand | Sand 5 Humus 1 | Humus | Clay |
|---|---|---|---|---|---|
| A. | Holes | 13 | 10 | 4 | 0 |
| | Larvae | 13 | 10 | 0 | 0 |
| B. | Holes | 15 | 24 | 1 | 2 |
| | Larvae | 15 | 11 | 1 | 0 |

the restricted and unnatural conditions of the experiments the animals showed a marked preference for clean white sand and a somewhat smaller preference for sand containing a small amount of humus. These two experiments were performed with much care to avoid errors due to the migration of larvae, and the results are the expression of the selection by the female. Other experiments were rejected because of the possibility of such errors. Each larva on hatching from the egg digs a hole at the point where the egg was laid and does not ordinarily migrate. However if conditions become unfavourable they leave their holes and migrate until they find moist sand like that in which the female laid the egg; here a new hole is made. After a two-day heavy rain, individuals were found on top of a small sand dune. The sand was wet on the dunes and no doubt flooded in the usual low places.

After a strong wind which covered the low places on the beach with a layer of dry sand, five larvae were seen wandering on the beach while the observer was walking a sixth of a mile. Thus the larvae maintain themselves in essentially the conditions in which the female laid the eggs.

The larvae feed on all sorts of insects and other minute animals that come within reach of their burrows. The newly hatched larvae feed for about a month, when each closes the entrance to its burrow and goes to the bottom and moults. It returns to the surface after about a week with a head and thorax of distinctly larger size. After feeding for another similar period it moults again and is then in the final larval stage. This is usually reached in September. In October they close their burrows and go to the bottom and remain inactive until April. The larvae open their burrows in May and feed until June or July, when each again closes the upper part of its burrow and constructs an oblique slender curved cavity near the bottom. After three weeks of semi-active larval life, the larva pupates in this cavity. It remains in the pupal stage for three weeks more when it becomes an adult by another moult.

Ordinarily it is not possible to bring the last larval stage through its transformations without the winter period. This can however be accomplished with some delay by raising the temperature to 36–40° C. The exact reason for this is unknown.

When the adult stage is reached (end of July) the insects dig to the surface before the cuticula is hardened and fly actively on the moist margin of the lake in favourable weather. They dig small burrows in the sand for nights and for cloudy days. After two or three weeks of activity they burrow into the higher drier parts of the beach, though the weather is still warm, and remain there until the following June when they dig out and resume activity as in the preceding autumn though they are still not sexually mature. I have not been successful in forcing newly emerged individuals to maturity by keeping them in a warm vivarium, but the experiments have thus far been of a preliminary nature. After wintering out of doors they reach sexual maturity and copulate on warm sunny days. It is evident that they undergo some change during the winter. The entire life cycle requires two years.

From this brief statement of the life history the following facts are evident. (1) The distribution and conditions of existence of the larvae and pupae are governed by (*a*) the selection of the egg-laying place by the adult and (*b*) the migration and selection of burrowing place by the larvae; (2) the various stages of the life history are characterized by special activities; (3) there is a nine month period of dormancy in the adults during which some physiological changes take place; (4) there is a six month period of dormancy in the larvae which is similar to the adult period.

3. **Dormancy.** Dormancy in eggs is a common thing among rotifers, crustacea, insects and probably a great many other arthropods. Many crustacea deposit eggs in the autumn that require winter freezing before they will hatch, while some require summer drying and winter freezing. The larvae and pupae of lepidoptera often require freezing before development will take place; Greely (**20**) found that desiccation could be substituted for freezing.

The eggs of the Rocky mountain locust require *time*, a certain amount of *warmth* in spring and probably a certain amount of *cold* in winter before development will proceed (**40**, pp. 137–140). In the polyzoa Braem found that freezing improved germination (**21**). In general the phenomena are essentially the same as in the seeds of plants.

4. **Factors.** Various single factors have been held as most important in the control of the distribution of organisms. Total temperature above an arbitrary minimum during the growing season has been held as important by some workers, of whom Merriam (**26**) is a notable example. This is indeed an important idea. Sanderson (**29**) has shown that for some insects and horticultural plants *winter* temperatures are more important. Vestal (**41**) emphasizes food in the case of animals of the Illinois sand prairie. Walker (**42**) emphasizes atmospheric moisture. The writer has pointed out the importance of recording complexes of factors such as the evaporating power of the air which measures moisture, air movement, temperature, light, and pressure. This is important particularly in dealing with the fauna as a whole, when different species are to some degree controlled by different factors. All the ideas stated have some truth in them and in fact most of them are important but none of them are complete or adequate. Any system that fails to consider the *complete physiological life history of each organism in relation to complete annual cycles* is inadequate, though the measure of conditions during sensitive periods is often of great value. Adequate measures of climates are to be found in the peculiar character of the animal rhythm rather than in totals of this or that factor for the year or particular periods.

Different workers working on different parts of physiological histories emphasize the factor that stands out at that period and very generally fail to emphasize those that have important bearings at other periods. Thus disagreements are always arising. Difficult as they may be, the final settlement of all such disputes will come after the investigation of a large number of physiological histories.

5. **Geographical variation in life histories.** Here we can compare animals of Manitoba with animals living near Chicago. We compare a point just east of Chicago where the climate is suitable for forest though almost at its western limit, with Aweme (near Brandon), Manitoba, where the climate is suitable for steppe (**34**).

TABLE II

*Showing comparative meteorological conditions in Chicago (lat. 42°) and Brandon (lat. 50°, 25 miles north-west from Aweme) during active period of tiger beetles* (Cicindela), *April to September, and during the time of digging hibernation burrows (September)*

| | Rainfall April to September. Inches | Total sunshine April to September. Hours | Mean max. temp. April to September. Deg. F. | Ratio of rainfall to evaporation. Per cent. | Mean temperature. Deg. F. | Mean maxima: September. Deg. F. | Mean minima: September. Deg. F. | Tot rainf Incl |
|---|---|---|---|---|---|---|---|---|
| Chicago | 19·3 | 1695 | 70 | 100 | 48 | 71 | 57 | 33· |
| Brandon | 12·45 | 1310 | 68 | 80 | 33 | 66·4 | 38 | 17· |

In S.W. Manitoba when compared with Chicago, the plant ecologist notes the dominance of short-stemmed plants, thicker cutin, succulence and other characters that tend to check evaporation, both in the flora generally and in the species occurring both at Chicago and in Manitoba.

In the case of the animals differences are less obvious. Suggestions as to some of the general differences in the tiger beetles will be found in Table III and in the discussion which follows.

TABLE III

*Showing the relative depths (in centimeters) of hibernation burrows of adults and burrows of larvae, of the same species, in the same or similar soil near Chicago and in S.W. Manitoba* (**11**). *Compare with Table II. Aweme is 25 miles east of Brandon*

| | Larvae | | | Adult hibernation | |
|---|---|---|---|---|---|
| | | Chicago | Brandon | | Chicago | Brandon |
| Species of *Cicindela* | Kind of soil | Depth of burrow | Depth of burrow | Kind of soil | Depth of adult in hibernation | Depth of adult in hibernation |
| *C. limbalis* | clay | 5–10 | 15–20 | clay | 5–8 | 7–15 |
| *C. tranquebarica* | sand ? | 22–50 | 43–50 | clay | 15 | 15–30 |
| *C. formosa* | sand | 30–50 | 125–200 | sand | — | 62–117 |
| *C. scutellaris lecontei* | sand | 25–45 | 70 | sand | — | 25–64 |
| *C. 12-guttata* | alluvial | 5–10 | 15–37 | clay | 10–15 | 5–25 |

We note on comparison that the larval burrows and the adult hibernation burrows are deeper under colder dryer Manitoba conditions. Criddle (**11**) noted that the larval life of some of the species common to Chicago and Aweme (near Brandon) is *two years* in Manitoba while near Chicago it is *only one year*.

Criddle states that in Manitoba there are often long intervals of inactivity of the larvae during the summer months. At such times they close their burrows at the top and remain apparently without food, and do not grow appreciably. In 1907, larvae of *Cicindela venusta* and *C. limbata* closed their

holes on June 12, and some did not appear again until August 25. A few, however, would open them at night, throw out a lot of earth and then retire again. These larvae were always active when dug out. He suggests further that this strange habit may be due to the dryness of the soil to some extent, though it is not altogether so, as holes have remained closed during wet weather, and they are always opened in autumn or late summer, and deepened before winter, no matter what the condition of the ground is. He states further that the extreme heat of the sun may also be a factor of some importance. The beetles are unquestionably influenced by temperature, and will go into winter quarters earlier on a dry, hot fall, than they do during a cold one, and hot summer days are much preferred for commencing winter homes.

In captivity the larvae of all species studied at Chicago close the burrows near the mouth and go to the bottom when the soil is dry. Here they remain inactive until water is applied. Thus the same thing occurs under *experimental* and comparable *climatic* conditions.

6. **Rhythms of conditions and rhythms of activity.** In animals as in plants there are various rhythms of activity constituting parts of their physiological life histories or recurring functions lying within them. These often coincide with various rhythms of conditions. Some determine distribution, some are tied up with dormancy and they are always clearly an important part of the physiology of environmental relations. The principal rhythms are tidal, daily, weather, lunar, and seasonal.

Bohn (**7**) found that there are rhythms of activity related to tide. For example the green flatworm *Convoluta roscoffensis* comes to the surface of the sand at low tide and descends when the tide comes in (**22**, p. 156). These and other animals manifesting such rhythms continued to act rhythmically after all the rhythmic conditions were withdrawn by removing them to aquaria. Daily rhythms are of common occurrence. Organisms such as crustacea of lakes congregate at the surface at night and migrate from the surface during the day (**14**). Lunar rhythms occur at certain seasons of the year in the case of certain marine worms (**24**). On the north Atlantic coast a clam worm (*Nereis limbata*) comes to the surface just after sunset, in general during the dark of the moon of June, July, August and September. Each swarm or "run" begins near the time of the full moon, increases to a maximum during successive nights, and falls to a low point about the time of the third quarter. It increases again but falls to extinction about the time of the new moon. During these runs the eggs and spermatozoa are cast into the water. Seasonal rhythms are illustrated by the life history of the tiger beetle given above.

## III. Structure in Ecology

1. **Response.** As was suggested in the introductory remarks, the more striking responses of *sessile* plants are changes in form and structure. All the chief characteristics of sessile plants are manifested by sessile marine animals. The growth form of some plants is distinctly paralleled by the growth form of sessile animals such as corals. The comparison is made clear in Fig. 4, *A–C* and *D–F*. There is some disagreement as to whether the growth forms shown in Fig. 4, *A–F* are hereditary or due to environment. However they represent characteristic differences which are doubtless due to environment in other species. These differences are comparable in many cases as will be seen by comparing Fig. 4, *G*, *H*, with Fig. 4, *I*, *J*.

The structural responses of motile animals are a legitimate part of ecology but at the same time belong more strictly to other branches of biological science. Fig. 4, *K–M* show the effect of creeping on the substratum during the growth of a new tail by a flatworm. Many such cases of response could be cited, but are quite familiar as a basis of some of the ideas of Lamarckism.

2. **Adaptation.** In animal ecology structural adaptation is usually conceived of as of secondary or tertiary importance. The most striking structural adaptations of terrestrial animals are found in subterranean, cursorial, and arboreal or other types of ectophytic life. Animals are cursorial, subterranean or arboreal in all the possible different kinds of situations and thus adaptation is with reference to the *vertical* conditions in which the animals live rather than to the climatic or other physical conditions which are usually horizontally arranged. This is evident when we compare desert, rain forest, and savanna; the primary ecological divisions are to a considerable degree out of relation with the adaptations, as burrowers, runners and climbers occur in all three habitats.

3. **Taxonomy.** Taxonomy is not a part of ecology but is a field nevertheless of much importance to the ecologist because (1) it supplies a necessary language; (2) each species has a more or less definite ecological constitution, and in so far as the ecological constitutions of species are known it is possible to draw ecological conclusions from mere lists of species which are inhabitants of given uniform sets of conditions. The physiological life histories of animals are all listed under the names of species. The use of species in ecology is however attended by grave danger of error because (1) some are made up of ecologically different "forms" as is illustrated by the isopods mentioned on the preceding pages; (2) geographically separated communities may be *ecologically similar* or almost identical and all or a large part of the species be *different*. Thus the steppes of America and Eurasia are occupied by ecologically similar animals which in almost no case belong

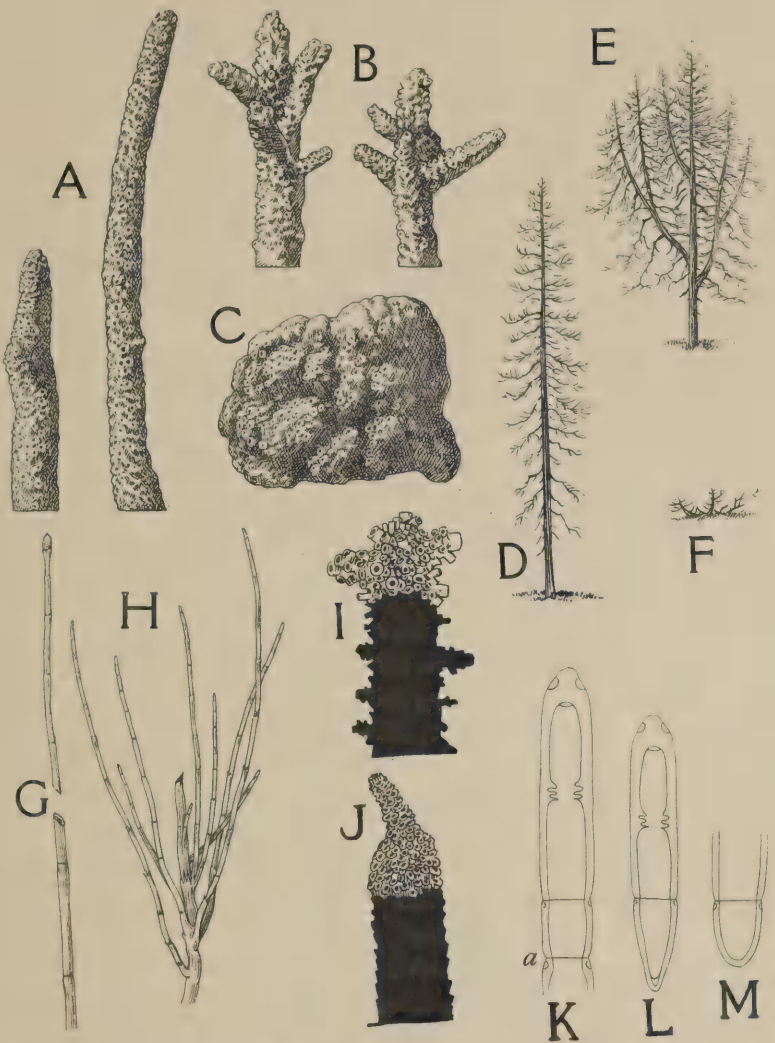


FIG. 4. *A*, *B*, *C*, growth forms of *Madrepora* growing under different conditions—*A* in deep water, *B* in barrier pools, *C* in rough water. *D*, *E*, *F*, growth forms of *Pinus montana*—*D* and *E* from mountain forest, *F* from mountain moor. *G*, *H*, showing the effects of injury to the leader or dominant individual on growth form in *Equisetum*—*G*, plant of protected situations with leader uninjured; *H*, the same from exposed sand dunes showing injury to the main stem and development of many lateral shoots. *I*, *J*, the repair of a *Madrepora* when the dominant zooid is not destroyed (*I*) and when it is destroyed (*J*). *K*, *L*, *M*, showing the effect of use and disuse on the growth of the tail of a flatworm (*Stenostoma*) which exists at certain seasons as chains of individuals; *K* shows a chain which was separated at the point *a*; a similar chain was separated at a similar point; in one case (*L*) the two anterior sections were permitted to creep with the posterior end in contact with the substratum and the tail became pointed after 8–9 hours, in another case (*M*) the tail was not allowed to attach and the tail remained rounded after 8–9 hours. *A–C*, *I*, *J*, after Wood-Jones; *D–F* after Schröter; *G*, *H*, after Cowles; *K–M*, after Child.

to the same species. Hence the study of ecology by means of species has its distinct limitations.

## IV. Animal Communities

1. **Physiological basis.** Plants and animals select their habitats through physiological characters. Sessile plants and animals have disseminules which usually come to rest in a great variety of conditions and grow to maturity only in those conditions that are suitable to stimulate development. The physiological character of the reproductive bodies and external conditions are responsible for the distribution of the adults. To some extent this is also true of the motile animals but their distribution is more generally controlled by the behaviour of the *motile* stages. The vast majority of motile animals turn back when they reach the outskirts of their usual environments. Further special activities take place in much narrower limits than general activities. This is illustrated by the breeding of the tiger beetles noted above (pp. 5, 6).

Some motile animals spend one season in one locality and another in another. Still, some of their activities take place within very narrow limits and are the centre about which all other activities rotate (see **34**). Such animals as migratory birds, contrary to statements sometimes made, are the best of ecological material because they are much influenced by conditions during the time of migration and thus show responses to all sorts of fluctuations. The ecological problems presented by such organisms are not essentially different from those of plants, the various rhythms of life history and response being evident through *migration* rather than *growth*.

Animals select their environments by one of three methods: (1) by wide dissemination of reproductive bodies and selective survival, (2) by turning back when the environment in which they move about is found to change, and (3) by selection after trial in connection with migration. Numbers of animals select the same environment because of physiological similarity. Agreement in behaviour and physiology among the animals of communities is to be expected, just as there is growth form agreement in plant communities. Thus selection of the same environment by many species is an aspect of the basis of animal communities (see **38**).

2. **Associational basis.** Prof. S. A. Forbes (see **15**) has kindly supplied the following statement regarding his method of determining the association of species in communities and a means by which he believes associations may be determined. "To recognize, analyze, and locate an association with precision, use is made of the obvious fact that a biological association is composed of species which are more frequently associated with each other than they are with other species, and hence that frequency of *joint*

*occurrence* of species in collections is a clue to their associate relationship. A certain chance frequency of joint occurrence will, however, result from an *indiscriminate* distribution of two species over the same area, although there may be no similarity of ecological relationship to bring them together; and this element of chance frequency must be eliminated before their frequency of ecological association can be distinguished."

"For a computation of the chance frequency of joint occurrence, there must be known the total number of collections ($a$) made over an area and by methods such that either or both species might have occurred in them; the number of collections actually containing each species ($b$ and $c$); and the number of collections ($d$) containing both species conjointly. Then $\frac{b}{a}$ expresses the chance that any collection of $a$ will contain the species the number of whose occurrences is represented by $b$; $\frac{c}{a}$ the chance that any collection will contain the species whose occurrence is represented by $c$; the product of these two fractions, $\frac{bc}{a^2}$, the chance that any collection will contain both species at once, provided that their distribution is indiscriminate, and $\frac{abc}{a^2}\left(=\frac{bc}{a}\right)$ the *probable* number of chance joint occurrences of the two species in the number of collections represented by $a$. Since $d$ represents the *actual* number of joint occurrences, $d \div \frac{bc}{a}\left(=\frac{ad}{bc}\right)$ expresses the ratio between chance occurrences and actual occurrences. If this ratio, called the *coefficient of association*, is approximately 1, no ecological association is indicated, but the joint occurrences are attributable to chance. If it is materially more than 1, such an ecological association is indicated; and if it is materially less than 1, a marked divergence of the species with respect to ecological relationship is to be inferred."

"The above computation, repeated for all the pairs of species which appear to have been most frequently taken together, until only those pairs remain whose coefficient is evidently 1 or less, gives the numerical data from which the existence and the composition of associations may be made out, and by which the strength or degree of the associative bond among the various species may be measured."

3. **Experimental demonstration of agreement of the animals of communities.** (*a*) *Aquatic communities.* To demonstrate the character of physiological agreement in animal communities, the societies of rapids and of pools of a stream were chosen. In a stream of small and medium size in rolling country, the bed is benched and pools and rapids alternate. Though the two types of situations are close together in space the communities

occupied by them are very different. A detailed study of the *rapids* community was made and the pool community compared with it in a few short tests (see **38**).

The controlling stimuli are largely mechanical. Reactions to current were tested in a straight current apparatus (Fig. 1). In their optimum current animals show greatest activity and efficiency. The optimum current for the pool community is about 4–6 cm. per sec. while the optimum for the rapids community is 16–20 cm. per sec. When the current is optimum the animals are able to maintain themselves in the stream, orient themselves with heads up stream (positive) and make progress up stream. In the rapids community there is a marked agreement in orientation. About 90 °/₀ of the trials were positive. In the pool community there is no general agreement in the reaction to current. Some species do not orient at all, but move in the direction headed. Others orient and move up stream if the current is very weak.

Reaction to bottom in the two communities is strikingly different. The tests were made in long narrow pans the bottoms of which were half stone and half sand. The pans were placed in a symmetrically lighted hood in a dark room and observed through a narrow slit. The rapids community animals which inhabit stones were very generally found on the stone bottom and avoided the sand to a corresponding degree. The animals of the pool community very generally preferred the sand and some of them burrowed into it. Another test of the rapids community animals consisted in substituting pans with the bottoms waxed throughout and with one-half of the bottom of the experiment overlaid with coarse quartz. The experiment was conducted in practically absolute darkness, a one candle-power incandescent lamp being flashed for the readings. Almost all the rapids animals were found on, under, or among the stones through a series of readings.

Reactions to light were tested with a Yerkes light grader. The reactions of the animals were found to be in agreement with the light conditions under which they live, i.e. whether on, under, or among stones.

Figs. 5 and 6 show a comparison of the two communities on scales of 300 and 400. The number of positive trials is graphically represented. It will be noted that animals of the rapids are in agreement in the matter of reaction to current all being strongly positive. They are further in agreement in the reaction to bottom. Their reaction to stones shows a difference with respect to being on, under, or above, which is in accord with the positions which the animals occupy in their native haunts. The reactions to light differ in the same manner and the rapids fishes which do not respond to light appear to be controlled to a considerable degree by kinesthesia. The pool community shows agreement in only one of the tests made—the reaction to sand bottom. The reactions to light were evident for only a part of the community;

burrowing was common to only a part. Only those that do not burrow react to current. This community is clearly *unsolved* and the agreement, except in the one respect, not clear from these tests, though other experiments have suggested that there is a great sensitiveness to the chemical character of the water.

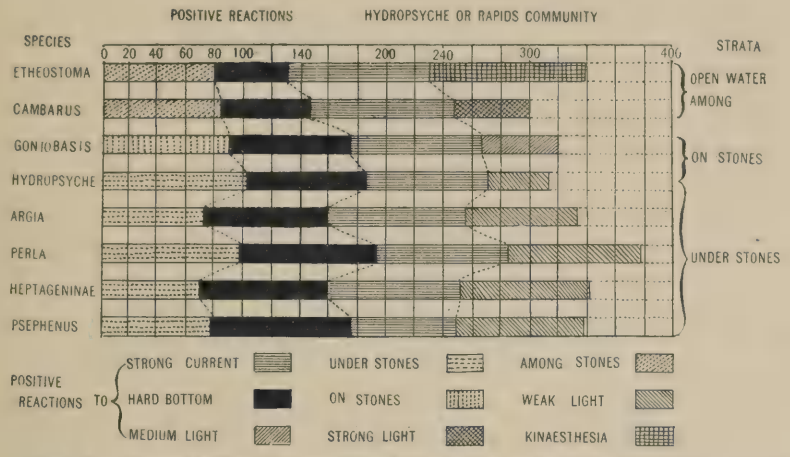


FIG. 5. Showing the agreement and disagreement of reaction of the rapids community. Note agreement of reaction to bottom and current and disagreement of two other reactions, related to the level at which the animals live. Each reaction is represented on a scale of 100 and if no other factors entered in the total should be 400 and the space all occupied.

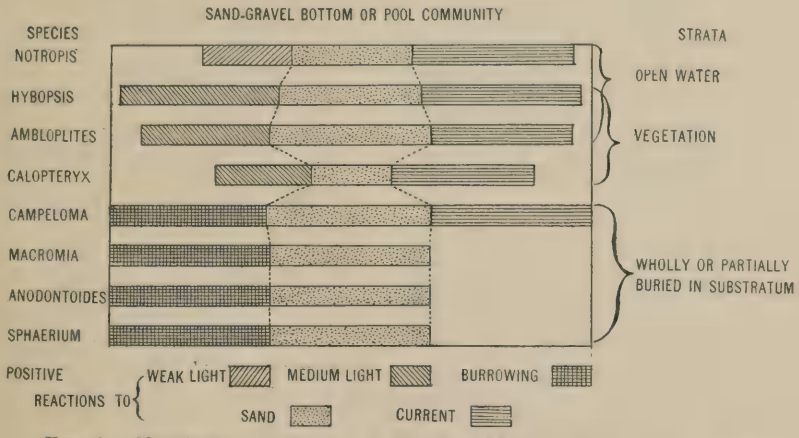


FIG. 6. Showing suggestions as to the probable agreement and disagreement of the reaction of the animals of the unsolved pool community on a basis of a total of 300, introduced to show the striking differences between communities.

There is clearly agreement in the rapids community in the reaction to stones and current. This agreement justifies terming the community litho-rheotactic. The disagreement is related to vertical separation, and the

animals living on stones, among stones, and under stones constitute *strata* and may be respectively designated as litho-phototactic, litho-pelagic, and litho-thigmotactic. Such a nomenclature could be applied where all the species are different from those occurring near Chicago, for example in England.

The agreement in the community is due (1) to the selection of the rapids community by the animals living there, due to similar innate characters; (2) to modification of behaviour by physical conditions; and (3) to the development of associative memory relating to the conditions in the community.

(*b*) *Land communities.* The writer has made a detailed study of the reaction of a few animals to variations in evaporating power of air. Air was supplied by a pump and forced across a long narrow shallow cage with a screen front and a glass cover. The air entered through a narrow slit from three fishtail-burner-shaped introducers. Each occupied a slit one-third of the length of the cage so that a different kind of air could be maintained in each third of the cage. Animals from the moist beech forest and from a cottonwood dune (dune dominated by *Populus deltoides*) were selected as representative of the communities occupying the two situations. The animals tend to go back and forth in the cages and to avoid one kind of air by staying in one end more of the time than in the other and by turning back on encountering avoided air.

(i) *Rating of the species studied.* In order to make comparisons it is necessary to estimate the degree of avoidance of air of the high or low rate of evaporation. In the main there are two indications of reaction; (*a*) *time spent in the two kinds of air* (*halves of the cages*) and (*b*) *number of turnings back on encountering the avoided air.* When both are expressed in terms of per cent. of total and the two regarded as of equal value, ratings can be obtained. Since the ratings are based upon a small number of experiments, they can be taken only as tentatively representing the relations of the animals to the rates of evaporation.

(ii) *Integument.* The animals were killed by rapid evaporation and fall into two distinct groups: (1) those dying with an evaporation varying from 0·07 to 4·8 c.c. from Livingston atmometers and after an exposure varying from 5 to 155 minutes, and (2) those dying with an evaporation of 31·0 to 42·0 c.c. after an exposure of from 1300 to 2200 minutes. The first group is made up of soft-skinned amphibians, the second of chitin-covered arthropods. Even though the arthropods were much smaller they lived from 8 to 450 times as long as the amphibians. The loss of water through a tracheal system should be at least as great as through the lungs; the difference is probably primarily due to the character of the integument.

(iii) *Reaction, survival-time, and habitat preference.* In general there

TABLE IV

*Showing the rating of the different species studied when the turnings back from the modified air and percent. of time in the two halves of the experimental cages are regarded as of equal value. The ratings are obtained from the percents. of total turnings from the halves and the percents. of time in the halves. The differences between the two percents. in each case were added and divided by 2. When the greatest number of turnings is from the end in which the least time was spent the turnings and time are of the same sign (+ or −)*

| | | | Experiments. Evaporation produced by | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Controls | | Dryness | | Movement | | Temperature | | Average | |
| Species and Habitat | No. | Rating | No. of Expts. | Rating | No. of Expts. | Rating | No. of Expts. | Rating | No. of Expts. | Rating |
| Beech Forest Animals: | | | | | | | | | | |
| Plethodon (Salamander) | 10 | ± 3·0 | 5 | −71 | 2 | −66 | 2 | −82 | 9 | −73 |
| Pterostichus (Beetle) | 1 | ±11·0 | 1 | −72 | — | — | — | — | 1 | −72 |
| Rana (Frog) | 19 | ± 1·5 | 5 | −68 | 2 | −80 | 2 | −69 | 9 | −72 |
| Dune Animals: | | | | | | | | | | |
| Microbembex (Wasp) | ·6 | ± 1·3 | 6 | + 6 | — | — | — | — | 6 | + 6 |
| Geolycosa (Spider) | 7 | ±10·0 | 4 | +18 | 2 | +16 | 2 | +12 | 8 | +15 |

is a rough relation between survival time and reaction among animals with *similar integuments*. Of the amphibians, the salamander died in dry air in 58 minutes and is rated at −73; the wood-frog died in 155 minutes and is rated at −72. Of the chitin-covered animals, the beetle (*Pterostichus*) is rated at −72 (single experiment) and died in 1300 minutes; the spider (*Geolycosa*), rated at +15, died in 2200 minutes.

The ratings clearly fall into two groups which are habitat groups (see Table IV). The beetles were taken from the surface of the ground under the leaves in a primeval beech forest; the spiders and wasps are regular residents of the driest open sand areas. The ratings compare favourably with the difference in evaporation in the two habitats. While a relation exists between habitat and survival time it is confined to animals with similar integuments. No such relation exists when one entire habitat group is compared with the other habitat group. The regular breeding residents of the two habitats (beech woods and open dunes) differ in sign and degree of behaviour *reaction* in a manner comparable with the difference in physical conditions of the habitats (see **37**). Distribution is then not a life and death matter for adults but a matter of behaviour reaction (see **34, 35, 36, 39, 43**).

A further comparison of the different species given in the table shows important relations to vertical conditions of forest developmental stages. The wood-frogs spend much of their time, during the day, hopping about the

forest floor. Salamanders live more of the time beneath the leaves and are more sensitive to evaporation.

4. **Innate characters of communities of different climates.** Something of innate ecological characters may be determined from literature. Take for example the mammals of Manitoba which have been quite fully treated by Seton (**32**). Manitoba is covered by three of the larger animal communities, those of (1) coniferous forest, (2) deciduous savanna, and (3) steppe. The strip of savanna divides the region into two parts along the N.W. and S.E. diagonal of the rectangular province. The area is thus rather geometrically divided into three ecological regions.

The mammals are listed below according to their life habits. The wapiti (or elk, near relation of the European red deer) and Virginia deer might perhaps be classified in the savanna, but since they are both cursorial they would thus only increase the contrast between the forest and steppe.

The following is a list of the chief animals arranged according to habitat. (1) *Forest species:*—elk (*Cervus canadensis*, Erxl.), deer (*Odocoileus virginianus borealis* Mill.), moose (*Alces americanus* Jard.), woodland caribou (*Rangifera caribou* Gm.), red squirrel (*Sciurus hudsonicus* Exl.), Canada woodchuck (*Marmota monax canadensis* Exl.), northern flying squirrel (*Sciuropterus sabrinus* Shaw), arctic deer mouse (*Peromyscus maniculatus arcticus* Mearns), Canada red backed vole (*Evotomys gapperi loringi* Bail.), Canada porcupine (*Erethizon dorsatum* Linn.), snowshoe rabbit (*Lepus americanus phaeonotus* Allen), Canada lynx (*Lynx canadensis* Kerr.), common weasel (*Putorius cicognanii* Bon.), marten (*Mustela americana abieticola* Preb.), fisher (*Mustela pennanti* Erxl.), grizzly bear (*Ursus horribilis* Ord.), black bear (*Ursus americanus* Pallas). (2) *Savanna species:*—mule deer (*Odocoileus hemionus* Raf.), common chipmunk (*Tamias striatus griseus* Mearns), little chipmunk (*Eutamias quadrivittatus neglectus* Allen), Franklin ground squirrel (*Citellus franklini* Sab.), jumping mouse (*Zapus hudsonius* Zim.), common shrew (*Sorex personatus* I. Geof. St Hil.), short-tailed shrew (*Blarina brevicauda* Say), skunk (*Mephitis hudsonica* Rich.), raccoon (*Procyon lotor* Linn.), red fox (*Vulpes regalis* Mer.). (3) *Steppe species:*—prong horn (*Antilocapra americana* Ord.), bison (*Bison bison* Linn.), yellow ground squirrel (*Citellus richardsoni* Sabine), striped ground squirrel (*Citellus tridecemlineatus* Mitch.), prairie deer mouse (*Peromyscus maniculatus bairdi* H. and K.), prairie red backed vole (*Evotomys gapperi loringi* Bailey), common meadow mouse (*Microtus pennsylvanicus drummondi* A. and B.), northern pocket gopher (*Thomomys talpoides* Rich.), jack rabbit (*Lepus campestris* Bach.), large weasel (*Putorius longicauda* Bon.), badger (*Taxidea taxus* Schr.), kit fox (*Vulpes velox* Say), gray wolf (*Canis occidentalis* Rich.), northern coyote (*Canis latrans* Say).

The ecological characters of the above animals are expressed in general terms in Table V.

We note that the steppe and forest species differ quite markedly while the savanna species are intermediate. In the steppe we note 70 °/₀ subterranean breeders as against 42 °/₀ in the forest; 47 °/₀ of the steppe animals live much of the time under ground while only 6 °/₀ of the forest species do so. The steppe shows 47 °/₀ gregarious, the forest but 16 °/₀. There is a close balance between the kinds of feeders in the steppe, and considerable

TABLE V

*Showing innate ecological characters of the mammals of three climatic communities in Manitoba*

| Activity | Stratum or other character | Forest species. Per cent. | Savanna species. Per cent. | Steppe species. Per cent. |
|---|---|---|---|---|
| Breeding | Arboreal | 26 | 10 | 0 |
| | Ground | 32 | 20 | 30 |
| | Subterranean | 42 | 70 | 70 |
| Habit of Life | Arboreal | 26 | 10 | 0 |
| | Ground | 68 | 40 | 53 |
| | Subterranean | 6 | 50 | 47 |
| Feeding | Herbivorous | 53 | 20 | 34 |
| | Omnivorous | 21 | 40 | 32 |
| | Carnivorous | 26 | 40 | 34 |
| Social | Gregarious | 16 | 30 | 47 |
| | Slightly gregarious | 26 | 20 | 12 |
| | Non-gregarious | 58 | 50 | 41 |

difference in savanna and forest probably due to a smaller number of rodents. Steppe animals are most gregarious. So far as records are given the speed of the steppe animals is greater than that of forest animals.

## V. Quantity of Life in Communities

The quantity of life varies in different communities and at different seasons in the same community.

1. **In water.** The amount has been much studied in the quantitative plankton studies. The number of animals varies as do the plants and the total quantity varies in accord with Liebig's Law of Minimum (see **3**, pp. 65–70, 302–303).

2. **On land.** Studies have been few and not clearly related to ecological associations. McAtee (**25**) found near Washington, D.C., 1,216,880 animals per acre of forest floor and 13,654,710 animals per acre of meadow. Forbes (**16**) found in Illinois 785 birds per square mile of forest and 1551 birds per square mile of pasture. Here plants and animals follow the same general rule.

## VI. Animal Succession

Succession of animals is as clear as that of plants. We recognize seasonal succession and ecological succession. Seasonal succession occurs in animals just as in the growth, flowering and fruiting of plants. It is due to hereditary differences in the physiological life histories of the animals occurring in a locality (see **5**; **23**, pp. 94–95). In land habitats there is often a close correspondence in maximum period of flowering and maximum number of animals in the adult stage.

Ecological animal succession is succession of ecological types over a given locality which takes place parallel with plant succession. It is due to topographic, climatic, and vegetational changes. Changes produced by the animals themselves are causes. Animals which burrow in the soil, such as earthworms, digger wasps, pocket gophers, etc., influence succession by influencing soil aeration and burying organic matter. It has also been shown that animals affect their surrounding conditions in manners detrimental to themselves. Some crustacea, snails, etc., are dwarted by their own excretory products (see **10** and citations). Woodruff (**44**) after a detailed study of the succession of Protozoa in infusions states that "emphasis is put upon the strictly biological inter-relations (i.e. those involving food and specific excretory products) of the various species as the most important determining factors in the observed sequence." Thus it seems evident that the causes of animal succession may include all those applying to plants. It is evident that the two go hand in hand because the agreement between animal communities and plant communities is evidently the rule.

## VII. Agreement of Plant and Animal Communities

Before discussing the problem of agreement between plant and animal communities, it is necessary to state what is meant by agreement. According to present developments of the science of ecology *plant and animal communities may be said to be in full agreement when the growth form of each stratum of the plant community is correlated with the conditions selected by the animals of that stratum.* Questions of agreement are primarily questions for experimental solution. Two types of disagreement are to be expected. We may illustrate the first by a bog or marsh community. Considering plants rooted in the soil we note that water is secured from the soil by the roots and is lost through the leaves and twigs. Accordingly since bog soil is unfavourable, due to the presence of toxins or to other causes, plants growing in it do not secure water easily even when the quantity of soil water is great. *Such plants have xerophytic structures (which tend to check the loss of water) developed far beyond the requirements of the atmospheric conditions surrounding their vegetative parts.* It is improbable that the animals inhabiting a bog vegetation field-stratum would *select* atmospheric conditions such as produce equally xerophytic structures under favourable soil conditions. We may therefore expect disagreement. The smaller plants, as fungi, algae, etc., are related to the strata of soil and atmosphere exactly as the smaller animals, and as much disagreement is to be expected between such plants and the rooted vegetation as between the rooted vegetation and animals. It must, however, be noted that the xerophytic structures of the plants of *unfavourable* soils may have important influence upon ectophytic plants and animals and in part counteract the effect of the favourable atmospheric conditions.

The second type of disagreement is represented by cases in which the vegetation is said to lag behind. Sometimes conditions become favourable for inconspicuous plants and forest animals as soon as the growth of the pioneer vegetation gives shade to the soil. In other cases woody vegetation remains in situations where the conditions have become unfavourable for it and the less conspicuous plants and some of the animals have disappeared. We may expect lack of accord within and between plant and animal communities under such conditions. In these cases, however, conditions are only temporarily out of adjustment due to rapid physiographic changes. Disagreements are often apparent only due to the emphasis of species, and no doubt such ideas as are abroad regarding disagreement between plant and animal communities grow out of the fact that many phytophaga are often less widely distributed than their food plants. In the absence of a general knowledge of the leaf responses of plants, zoologists jump to the conclusion that the plant is the same and the animal does not follow it.

## VIII. RELATIONS OF ECOLOGY TO OTHER BIOLOGICAL SUBJECTS

On the zoological side it is evident that the relations of ecology to other biological subjects are important. The most important biological problems of nearly all pest species and of the rearing of semi-wild animals are problems of physiological life histories. The efforts at control of pests are often aimed at some weak point in the life history. Attempts at increasing the numbers of fish and other useful animals are attempts to bridge over the weakest points in their life histories. The weak points in life histories are of special importance in ecology.

One of the central aspects of modern biology is the attempt to analyze the physical and chemical mechanism of the life process. Progress thus far has been chiefly along the line of the study of responses of living matter. Responses are the chief material of modern ecology, and the ecologist by no means necessarily stops with descriptions of superficial phenomena but may on the other hand push his enquiry as far as scientific methods will permit. The point of view of ecology is merely that of phenomena of physiology of environic relations manifested by organisms mainly in a wild state. In all its activities ecology is an attempt to catalogue, correlate, organize and analyze the phenomena of the physiology of environic relations.

UNIVERSITY OF ILLINOIS,
URBANA, ILL.,
*December* 1914.

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